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Chromosomes of *Bipes, Mesobaena,* and Other Amphisbaenians (Reptilia), with Comments on Their Evolution

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ABSTRACT

Karyotypes of three amphisbaenians (*Bipes tridactylus,* the monotypic *Mesobaena,* and *Amphisbaena gonavensis*) are presented for the first time. The karyotypes of all three species of *Bipes* are compared, using new material for each species, and all published karyotypes for representatives of the Amphisbaenia (approximately 20% of the Recent species, worldwide) are reviewed. Diploid chromosome numbers vary from 25 to 50, and centric fission of macrochromosomes appears to have been a major type of karyotypic evolution in these animals. *Bipes tridactylus* is the only amphisbaenian known to have recognizable sex chromosomes, with a ZZ(♂):ZW(♀) system (female heterogamety).

INTRODUCTION

The Amphisbaenia are a group of perhaps 150 Recent species of squamate reptiles that are highly specialized for burrowing. There are four families of uncertain affinities and ages, but clearly the Amphisbaenia are an ancient group related to lizards and snakes; the group is probably monophyletic, and it may be the sister group of Sauria (Gans, 1978).

To date, chromosome data for about 30 species of amphisbaenians have been published. Diploid chromosome numbers range from 25 to 50 (reviewed in Gans, 1978), and this, together with the significant variation in chromosome morphology suggests that additional understanding of amphisbaenian karyotypes may improve knowledge of their relationships and evolutionary history. In this paper we review all the karyotypic data avail-

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able for the Amphisbaenia after presenting new data concerning the following five species from Mexico, Colombia, and the Dominican Republic: the three species of Bipedidae (*Bipes*); the monotypic *Mesobaena* (*M. huebneri*); and *Amphisbaena gonavensis leberi.*

Acknowledgments

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METHODS

Chromosomes were prepared as described elsewhere (Cole, 1978), including in vivo preparations from bone marrow (vertebrae), testes, spleen, intestine, and whole blood, as well as in vitro cultures of whole blood. For small amphisbaenians that have been transported over thousands of miles and perhaps under trying conditions prior to processing several weeks or more after capture, it is best to try a variety of tissues and even at that, some preparations fail completely. Although amphisbaenians are most admirable in many respects, at least one of us can say "they surely are not my favorite animal!"

Specimens Examined

The specimens are individually cataloged in the herpetological collections of the American Museum of Natural History (AMNH) or the private collection of Carl Gans (CG), as follows:

Bipes biporus: MEXICO: *Baja California Sur:* El Sombrero Trailer Park, La Paz (AMNH 113486, ♂).

Bipes canaliculatus: MEXICO: *Guerrero:* Rio Balsas at Mexico Hwy. 95 (AMNH 113487, ♀; CG 5524, ♀; CG 5525, ♂; CG 5527, ♀).

Bipes tridactylus: MEXICO: *Guerrero:* 7 km (by Mexico Hwy. 200) SE Tecpan de Galeana (AMNH 113488, ♂; CG 5261, ♂; CG 5528, ♀; CG 5529, ♀; CG 5530, ♀).

Mesobaena huebneri: COLOMBIA: *Vaupes:* Timbo (AMNH 115936, ♀; AMNH 115937, ♀).

Amphisbaena gonavensis leberi: DOMINICAN REPUBLIC: *Pedernales Prov.:* 3.5 km WNW Oviato (Nuevo) (AMNH 113478, ♂; AMNH 113484, ♂).

KARYOTYPES

Bipes biporus: Examination of two cells from one male revealed a diploid number of 42 ($2n = 42$), with 20 macrochromosomes and 22 microchromosomes. These can be arranged in pairs and numbered in order of decreasing length (fig. 1A). Of the macrochromosomes, numbers 3 and 10 are metacentric or nearly so, numbers 1 and 7 are submetacentric and numbers 2, 4, 5, 6, 8, and 9 are subtelocentric. Generally the microchromosomes are too small to be resolved clearly, but at least two are biarmed. Neither secondary constrictions nor satellites were observed. This karyotype is the same as the one reported for this species by Huang and Gans (1971) and Macgregor and Klosterman (1979), allowing for insignificant differences in arranging and numbering the macrochromosomes.

Bipes canaliculatus: Examination of 13 cells from four individuals (1 male, 3 females) revealed a karyotype different from that of *B. biporus.* The diploid number of chromosomes is 46, with 22 macrochromosomes and 24 microchromosomes (fig. 1B). Of the macrochromosomes, numbers 1 and either 8 or 9 (designated no. 8 here; these are similar in size) are submetacentric and the rest are subtelocentric (no. 11 often appearing telocentric). Usually two microchromosomes appeared biarmed, but as many as six were so in some cells. No secondary constrictions, satellites, or sex-correlated chromosomes were observed. This karyotype is similar to the one reported for this species by Macgregor and Klosterman (1979), allowing for an insignificant difference in arranging and numbering of the macrochromosomes, except they reported only 22 microchromosomes ($2n = 44$) instead of 24 ($2n = 46$).

Bipes tridactylus: Examination of 40 cells from five individuals (2 males, 3 females) revealed that this species differs karyotypically from both *B. biporus* and *B. canaliculatus,* although the number of chromosomes

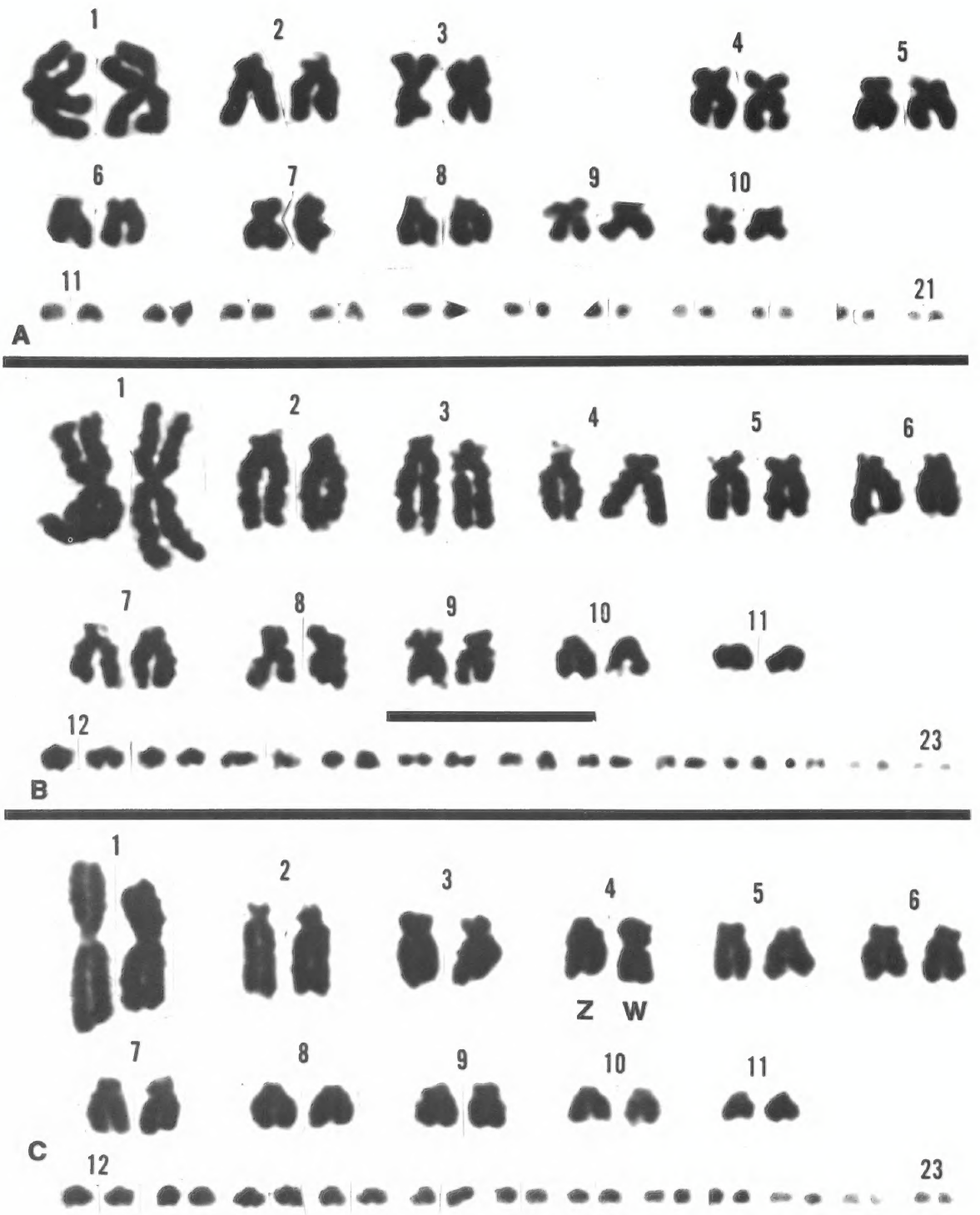

Fig. 1. Karyotypes of the three species of *Bipes*. **A.** *B. biporus*, $2n = 42$, AMNH 113486, male. **B.** *B. canaliculatus*, $2n = 46$, CG 5525, male. **C.** *B. tridactylus*, $2n = 46$, CG 5528, female with heteromorphic pair number 4. Only the largest and smallest pairs of microchromosomes are numbered. Line in B represents 10 microns.

is similar to the latter. The diploid number is 46, with 22 macrochromosomes and 24 microchromosomes (fig. 1C). Of the macrochromosomes, number 1 is submetacentric, numbers 2 and 3 are subtelocentric, numbers 5 through 11 are subtelocentric to telocentric, and number 4 is a pair of sex-correlated chromosomes that are heteromorphic in the females (one subtelocentric to telocentric, one submetacentric) but homomorphic in the males (subtelocentric to telocentric). Thus, this species apparently has a ZZ(♂):ZW(♀) sex chromosome system (fig. 1C). Usually a few microchromosomes appeared biarmed, and neither secondary constrictions nor satellites were observed.

Mesobaena huebneri: Examination of 15 cells from two females revealed a diploid number of 46 chromosomes, with 24 macrochromosomes and 22 microchromosomes (fig. 2A). All of the macrochromosomes are telocentric, except number 1, which is subtelocentric. The number of microchromosomes appearing biarmed did not exceed five in any cell. No secondary constrictions, satellites, or sex-correlated chromosomes were observed.

Amphisbaena gonavensis leberi: Examination of nine cells from two males revealed a diploid number of 50 chromosomes, with 22 macrochromosomes and 28 microchromosomes (fig. 2B). Of the macrochromosomes, number 1 is metacentric or nearly so, numbers 2, 3, and 4 are submetacentric, and the rest are telocentric. No more than four microchromosomes appeared biarmed in any cell. In two cells, a single microchromosome appeared to have a secondary constriction, but they were not sufficiently clear and consistent for firm conclusions about their location.

DISCUSSION AND CONCLUSIONS

With somatic chromosome numbers among amphisbaenians ranging from 25 to 50, one might readily question whether some species are polyploids. Review of all published karyotypes, however, indicates that all species are diploid (table 1). Some species have considerably fewer microchromosomes than others, but the most conspicuous differences in numbers are in macrochromosomes. Species with the fewest macrochromosomes have the largest ones and these are biarmed (including many metacentrics), whereas species with the most macrochromosomes have smaller ones that are largely uniarmed (telocentric or subtelocentric). This suggests that fusion or fission of macrochromosomes has been a major component of karyotypic evolution in amphisbaenians (Huang et al., 1967).

Using in-group and out-group comparisons, including complete representation within pertinent groups, and comparing such karyotypic details as total number of chromosomes, number of chromosomes within the different size-groups, and positions of useful markers (centromeres and satellites), reasonable hypotheses can be proposed regarding the direction of karyotypic evolution, including fusion or fission of macrochromosomes (Huang et al., 1967; Lowe et al., 1970; Huang and Gans, 1971; Webster et al., 1972; Cole, 1974; Paull et al., 1976; Sites, 1983; Porter and Sites, 1985). With such details in mind, we examined all published photographs of karyotypes of amphisbaenians (table 1). The resulting conclusions, mostly supporting Huang et al. (1967), and predictions are enumerated and discussed below. A few of our statements concerning chromosome numbers or morphology differ slightly from those of the authors or photographs cited, but such differences are intended, due to our reinterpretation of certain material.

1. Good photographs of karyotypes have been published for 30 species (approximately 20%) of the Recent Amphisbaenia. Of these, 18 species (60%) have six pairs of clearly biarmed (metacentric or submetacentric) macrochromosomes.

2. Not only do most species have six pairs of large biarmed chromosomes, but in all of these species, the macrochromosomes are the same relative sizes and shapes (Huang et al., 1967, pp. 11, 12). Chromosome numbers 1 (metacentric) and 2 (submetacentric) are clearly the largest and similar to each other in size; numbers 3, 4, and 5 are the next largest and similar to each other in both size and shape (metacentric); and number 6 (submetacentric) is the smallest of the macrochromosomes. No sexually dimorphic chromosomes are included and neither secondary

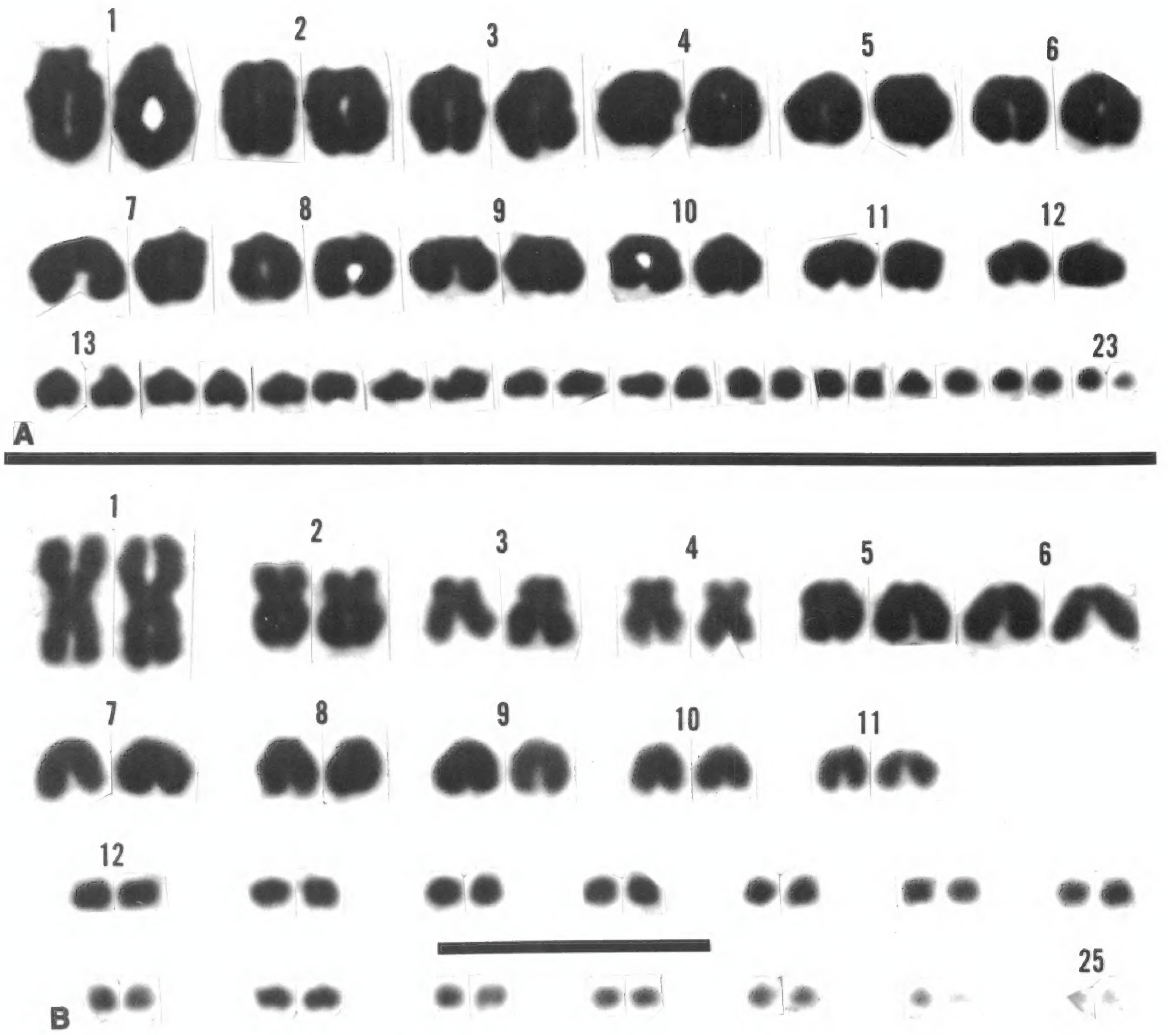

Fig. 2. Karyotypes of two amphisbaenians. **A.** *Mesobaena huebneri,* $2n = 46$, AMNH 115937, female. **B.** *Amphisbaena gonavensis leberi,* $2n = 50$, AMNH 113484, male. Only the largest and smallest pairs of microchromosomes are numbered. Line in B represents 10 microns.

constrictions nor satellites have been reported.

3. Furthermore, the above condition (point 2) is found in species from all the major geographical regions represented in the overall sample in the Eastern and Western Hemispheres; these karyotypic details are shared by representatives of half of the families (all the Trogonophidae, from Morocco and Saudi Arabia; most of the Amphisbaenidae, including some from Turkey, western Africa, South Africa, Argentina, Brazil, and Haiti); and this condition occurs in species judged on other characters as "probably the most primitive living species" (Gans, 1978, p. 401; referring to the species of *Blanus* in table 1), as well as the most primitive of the acrodont forms, *Trogonophis* (see Gans, 1978, p. 362).

4. We conclude that the karyotypic state of macrochromosomes described in point 2 above occurred in the common ancestor from which the Recent Amphisbaenia evolved; in other words, it represents the ancestral or primitive state for the Amphisbaenia. Deviations from this condition in amphisbaenians were derived from it.

TABLE 1
Amphisbaenians of Which Karyotypes Have Been Illustrated

Taxon	Provenance	Chromosomes[a]	Reference[b]
Trogonophidae:			
Diplometopon zarudnyi	Saudi Arabia	36 (12 + 24)	1
Trogonophis wiegmanni	Morocco	36 (12 + 24)	1
Amphisbaenidae:			
Amphisbaena fenestrata	Virgin Islands	36 (12 + 24)	2
A. manni	Haiti	36 (12 + 24)	2
Zygaspis quadrifrons	southern Africa	36 (12 + 24)	1, 2
Z. violacea	South Africa	36 (12 + 24)	2
Leposternon microcephalum	South America	34 (12 + 22)	1, 3, 4
Monopeltis capensis	South Africa	34 (12 + 22)	2
Chirindia langi	South Africa	?34 (12 + ?22)[c]	2
Blanus cinereus	—	32 (12 + 20)	1
B. strauchi	Turkey	32 (12 + 20)	1
Cynisca leucura	western Africa	?32 (12 + ?20)[c]	2
Amphisbaena angustifrons	Argentina	30 (12 + 18)	1
A. darwini	Uruguay	30 (12 + 18)	1
A. heterozonata	Argentina	30 (12 + 18)	1
A. trachura	Brazil	30 (12 + 18)	1
A. dubia	Brazil	?28 (?12 + 16)[d]	3, 4
Anops kingi	Brazil	26 (12 + 14)	2
Geocalamus acutus	Kenya	38 (14 + 24)	2
Amphisbaena alba	South America	38 (22 + 16)	2, 3
A. vermicularis	Brazil	44 (22 + 22)	4
A. fuliginosa	Trinidad	48 (22 + 26)	2
A. gonavensis	Hispaniola	50 (22 + 28)	5
A. innocens	Hispaniola	50 (22 + 28)	2
A. camura	Paraguay	44 (24 + 20)	1
Mesobaena huebneri	Colombia	46 (24 + 22)	5
Bipedidae:			
Bipes biporus	Mexico	42 (20 + 22)	1, 2, 5, 6
B. canaliculatus	Mexico	46 (22 + 24)	5, 6
B. tridactylus	Mexico	46 (22 + 24)	5
Rhineuridae:			
Rhineura floridana	United States	44 (22 + 22)	1

[a] Diploid number (macrochromosomes + microchromosomes).

[b] 1 = Huang et al., 1967; 2 = Huang and Gans, 1971; 3 = Becak et al., 1972; 4 = Benirschke and Hsu, 1973; 5 = this report; 6 = Macgregor and Klosterman, 1979.

[c] Precise number of microchromosomes not clearly resolved.

[d] An interesting tissue polymorphism with counts of 25 through 28 was reported by Becak et al., 1972.

5. The number of microchromosomes varies from 7 to 14 pairs. These are tiny chromosomes (on the order of one micron or smaller), the morphology of which is generally poorly resolved. As many (9) of the 18 species with the primitive macrochromosomes have 11 pairs (3 species) or 12 pairs (6 species) of microchromosomes, and as 11 or 12 pairs of microchromosomes occur in representatives of all families (including all Bipedidae and Rhineuridae), we conclude that the ancestral macrochromosomes discussed in points 2 and 4 above were accompanied by 11 or 12 pairs of microchromosomes in the primitive karyotype. Deviations from the ancestral number of microchromosomes usually are difficult to explain because microchromosomes are small and difficult to resolve.

6. Nine species have a shared-primitive

karyotype (see table 1 for correlated information), including *Diplometopon zarudnyi* and *Trogonophis wiegmanni* of the Trogonophidae and the following species of the Amphisbaenidae: *Amphisbaena fenestrata, A. manni, Zygaspis quadrifrons, Z. violacea, Leposternon microcephalum, Monopeltis capensis,* and *Chirindia langi.* Major derivations from this karyotype are discussed below.

7. A few of the species listed in point 6 merit additional comment. In *Monopeltis capensis* (see Huang and Gans, 1971, fig. 5), it appears that the largest submetacentric chromosome (no. 2) has a relatively longer short arm than in the other species, even allowing for minor rearrangements in the way the macrochromosomes were presented; this may apply also to the two species of *Zygaspis.* Future workers may investigate whether these species, and others in Africa (particularly additional species of *Monopeltis*) share a derived chromosome number 2, perhaps resulting from an unequal pericentric inversion or a centromere shift.

8. The two species of *Blanus* (from the Iberian Peninsula, Morocco, and Asia Minor) share the primitive karyotype with but one modification; each has 10 pairs of microchromosomes instead of 11 or 12. Similarly, *Cynisca leucura* of western Africa differs karyotypically from the ancestral condition only by reduction in number of microchromosomes (9 or 10 pairs).

9. Five species from South America (specimens from Argentina, Brazil, and Uruguay) also differ karyotypically from the ancestral condition only by reduction in number of microchromosomes. There are nine pairs in *Amphisbaena angustifrons, A. darwini, A. heterozonata,* and *A. trachura,* which may be a shared-derived condition uniting these species. The more extreme reduction in the monotypic *Anops kingi* (to seven pairs of microchromosomes) may be independently derived from the ancestral condition or may reflect further derivation from a common ancestor it shared with the four species of *Amphisbaena* just listed.

10. Obvious and relatively easily explained modifications of the macrochromosomes from the primitive states (point 2 above) involve centric fission (see discussion in Cole, 1974), which has included, depending on the example, one, five, or all six pairs of macrochromosomes.

11. *Geocalamus acutus* from Kenya provides the only published example of apparently simple macrochromosomal fission in the Eastern Hemisphere. The fission is of ancestral chromosome number 5 only. Otherwise, the karyotype of this species is the same as the primitive one (Huang and Gans, 1971, fig. 10). If the same karyotype occurs in *Geocalamus modestus,* this could be useful as a shared-derived character.

12. *Mesobaena huebneri* (from Colombia) and *Amphisbaena camura* (from Paraguay) have similar karyotypes that essentially differ from the ancestral one only in fission of the macrochromosomes, but in these extreme cases, each of the macrochromosomes has undergone fission to telocentric chromosomes. Considering other characters of these species, we propose that this is an example of karyotypic convergence, fission of all the macrochromosomes having occurred independently in their two separate clades.

13. Considering that some species in the Western Hemisphere apparently have all the macrochromosomes derived through fission into telocentric chromosomes, it would not be surprising to find intermediate stages of this derivation in this hemisphere, equivalent, for example, to that which *Geocalamus acutus* represents in Africa (point 11 above). Such may be exemplified by *Amphisbaena vermicularis* (from Brazil) and *Rhineura floridana* (from Florida, U.S.A.). These two species have essentially identical karyotypes, with only one pair of metacentric macrochromosomes. This pair is about equivalent in size and shape to number 4 in the ancestral karyotype (point 2 above), and may be homologous with number 4, whereas all the other macrochromosomes may have been derived by fission. Convergence may be the easiest explanation for the karyotypic similarities observed in these two species of different families from different continents. However, one should definitely consider whether the similarly highly derived karyotypes of *A. vermicularis* and *A. camura* (point 12 above) do indeed share many fission events in one clade.

14. The four remaining species of *Am-*

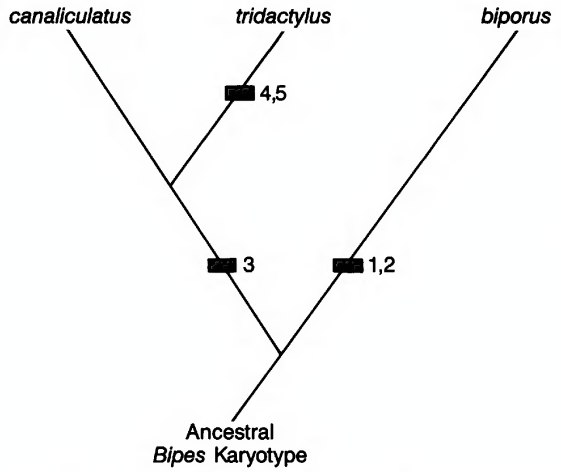

Fig. 3. Preferred cladogram for the species of *Bipes,* based on their karyotypes. The ancestral state for the genus was derived from that for the suborder by centric fission of macrochromosomes (see text, points 15 and 16). Additional derived characters proposed (text point 16) are the following: (1) change in position of centromere of pair 10; (2) apparent loss of a pair of microchromosomes; (3) centric fission of pair 3; (4) change in position of centromere of sex chromosome W, pair 4; and (5) change in position of centromere of pair 8.

phisbaena for which there are chromosome data are karyotypically derived in complicated fashion involving more than simple fission of the macrochromosomes. Although sizes and shapes indicate that fission was involved extensively, several to many of the macrochromosomes are clearly biarmed (subtelocentric and submetacentric), suggesting the fixation of unequal pericentric inversions, centromere shifts, or the addition of heterochromatin following the fission events (see Huang and Gans, 1971, figs. 11–13; fig. 2B here). These four species (*A. alba, A. fuliginosa, A. gonavensis,* and *A. innocens*) are a geographically coherent group from Caribbean islands, Trinidad, and northern South America. In two of these species, *A. gonavensis* and *A. innocens,* the karyotypes are essentially identical, with one very large metacentric pair (perhaps the unfissioned no. 1 pair of the ancestral state) and three pairs of the remaining 10 pairs of macrochromosomes being secondarily biarmed (following fission of ancestral pairs 2 through 6). This similarity probably reflects common ancestry in *A. gonavensis* and *A. innocens,* and the presence of an unfissioned pair of macrochromosomes may indicate that these species are less derived than the other two species in this series. Presence of the ancestral karyotype (point 2 above) in the similar *A. manni* from Haiti (table 1) suggests that this fissioning occurred in the Caribbean region. The karyotypes of *A. fuliginosa* and *A. alba,* respectively, appear progressively more derived, as evidenced by fission of ancestral macrochromosome number 1, increased number of secondarily biarmed macrochromosomes (but smaller ones, due to fission), and reduced number of microchromosomes.

15. The three species of the Bipedidae remain to be discussed. These also are karyotypically derived in complicated fashion involving more than simple fission of the macrochromosomes. Again, although sizes and shapes indicate that fission was involved extensively, many of the macrochromosomes are clearly biarmed (mostly subtelocentric), suggesting the fixation of unequal pericentric inversions, centromere shifts, or addition of heterochromatin following the fission events (fig. 1). The outcome of these events has been the evolution of three different, yet basically very similar, karyotypes in the three species of Bipedidae.

16. The macrochromosomes of *Bipes* differ so much from the ancestral states (point 2 above) that it is impossible to discuss homologs with the ancestral karyotype with certainty. Nevertheless, we offer the following hypotheses, summarized in figure 3, for future investigators to test: (a) the large submetacentric chromosome (no. 1 in all *Bipes*) is homologous in all three species and is homologous with the large submetacentric number 2 chromosome of the primitive karyotype, which makes it a shared primitive character in all *Bipes;* (b) the only other unfissioned macrochromosome remaining from the ancestral karyotype may be the large metacentric (no. 3) in *B. biporus,* which is of approximately the right morphology to be homologous with the ancestral number 5 (point 2 above); (c) thus, the primitive karyotype of the family Bipedidae may have been similar to that of *B. biporus,* but *B. biporus* is derived in having a fixed unequal pericen-

tric inversion (or centromere shift?) in its smallest macrochromosome and perhaps in having a reduction of microchromosomes by one pair (compare figs. 1 and 3); (d) *B. canaliculatus* and *B. tridactylus* share a derived fission of the ancestral number 5 metacentric macrochromosome (no. 3 in *B. biporus*); and (e) *B. tridactylus* is further derived in having a fixed unequal pericentric inversion (or centromere shift?) in its eighth (or so) largest pair of macrochromosomes plus having incorporated an unequal pericentric inversion in the female sex chromosome (W).

17. The strong similarities of the bipedid karyotypes do not allow firm resolution of the problems concerning their interspecific relationships (Kim et al., 1976; Papenfuss, 1982), but they are consistent with recognizing these three species as comprising a monophyletic group. The relative stability of the karyotypes within this group is in strong contrast to the extensive genetic differentiation indicated by protein electrophoresis, which may have occurred over a period of 4 to 15 million years (Kim et al., 1976).

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